

## SEX-BIASED PREDATION BY WEB-SPINNING SPIDERS (ARANEAE) ON SPRUCE BUDWORM MOTHS

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### ABSTRACT

Web-spinning spiders of 6 families, 12 genera, and at least 15 species preyed on spruce budworm, *Choristoneura fumiferana* (Clem.), moths in Maine. Significantly more ( $G$ -tests,  $P \leq 0.05$ ) male than female moths were captured by 9 web-spinner species, and the overall capture by spiders was significantly biased ( $P \leq 0.001$ ) toward male moths. Most of the budworm-moth prey were found in webs of *Frontinella pyramitela* (Walck.) (30.6%) and *Theridion pictum* (Walck.) (45.0%). Multiple observations of the same web (temporal replication) indicated that *T. pictum* captured significantly more ( $Z = -4.36$ ,  $P = 0.000$ ) budworm moths/web than *F. pyramitela*. However, such differences in prey-capture rates were not detected ( $Z = -1.49$ ,  $P = 0.14$ ) over several locations (spatial replication). Web surveys during the spruce budworm's moth-flight period indicated that percentages of webs with budworm prey were about equal; *F. pyramitela* ( $\bar{X} = 19.5 \pm 5.7$ ), *T. pictum* ( $\bar{X} = 18.9 \pm 3.6$ ), all species ( $\bar{X} = 16.0 \pm 2.7$ ).

Trees occupied by *T. pictum* were significantly taller ( $P \leq 0.001$ ) and webs significantly higher ( $P \leq 0.001$ ) than trees and webs of *F. pyramitela*. For both spider species, mean relative web height was  $> 60\%$  of tree height, possibly indicating nonrandom choices of foraging patch. However, tree height and web height were not significantly ( $P \geq 0.05$ ) related to prey-capture for *F. pyramitela* webs; tree height was significantly taller ( $P = 0.009$ ) for *T. pictum* webs with budworm moths. Two species of kleptoparasites, *Argyrodes trigonum* (Hentz) and *A. ficitium* (Hentz), were associated with host-spider webs that captured spruce budworm moths.

Possible explanations for the observed sex-biased predation include: 1) sex-pheromone mimicry, 2) uneven prey densities, 3) accidental capture, 4) moth behavior, and 5) moth-flight activity. Because of the potential impacts on spruce budworm reproduction, predation by spiders gains increased importance as a source of moth mortality.

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## INTRODUCTION

The spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae), is the most destructive defoliator of coniferous forests in the northeastern United States and Canada (Kucera and Orr 1981). Recent devastating outbreaks of this forest pest have renewed interest in determining the natural enemies—pathogens, parasites, and predators—that cause mortality to the spruce budworm. Spiders have long been recognized as predators of the spruce budworm (Johannsen 1913; Tothill 1923). Although all life stages of the spruce budworm—eggs, larvae, pupae, and moths—are susceptible to predation by spiders (Jennings and Crawford 1985), most observations concern spiders feeding on budworm larvae (Jaynes and Speers 1949; Loughton et al. 1963; Renault and Miller 1972). Few investigators have focused attention on spiders that prey on spruce budworm moths; Jennings and Crawford (1985) listed 10 species of web-spinning spiders that captured moths of *C. fumiferana* in their webs in Maine. Turnbull (1956) observed predation by both web-spinning and vagrant spiders on budworm moths in British Columbia; however, his observations pertain to the western spruce budworm, *C. occidentalis* Freeman.

In this paper we describe predation by several species of web-spinning spiders on moths of *C. fumiferana* in Maine, compare differential mortality between moth sexes, and discuss possible factors that contribute to sex-biased predation on male moths.

## METHODS

**Study sites.**—All observations were made in spruce-fir (*Picea-Abies*) forests that were infested with the spruce budworm. Individual study sites were distributed in a band from northwestern to southeastern Maine (Fig. 1). Study-site abbreviations, locations (by organized town or township), and observation years were:

- (SOL)—Soldiertown Twp., T2 R3, Somerset County, 1979.
- (WES)—West Middlesex, Canal Grant, Somerset County, 1979.
- (TOM)—Tomhegan Twp., Somerset County, 1979.
- (KOK)—Kokajo, T1 R13 WELS, Piscataquis County, 1977.
- (GRE)—NE of Greenville, T2 R12 WELS, Piscataquis County, 1978.
- (SHA)—Shawtown Twp., Piscataquis County, 1979.
- (TEL)—Telos, T5 R11 WELS, Piscataquis County, 1978.
- (COF)—Coffeelos, T6 R11 WELS, Piscataquis County, 1978.
- (MIL)—Milo, Piscataquis County, 1979.
- (MED)—Medford, Piscataquis County, 1978, 79, 80, 81.
- (HOW)—Howland, Penobscot County, 1978, 79, 80.
- (PAS)—Passadumkeag, Penobscot County, 1979.
- (PEF)—Penobscot Expmt'l Forest, Bradley, Penobscot County, 1978, 79, 80, 81, 82.
- (MAT)—Mattakeunk, Lee, Penobscot County, 1979.
- (STE)—West of Steuben, T7 SD, Hancock County, 1985.
- (T19)—T19 ED BPP, Washington County, 1979.
- (T18)—T18 ED BPP, Washington County, 1979.
- (P14)—No. 14 Plantation, Washington County, 1979, 81.

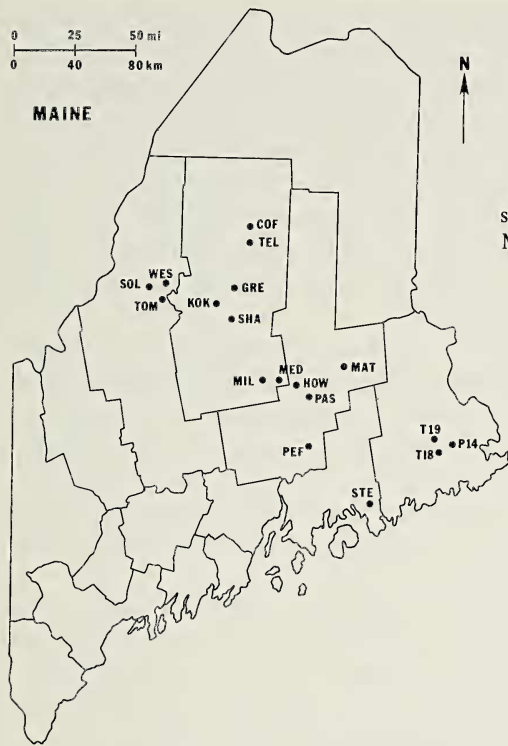


Figure 1.—Study-site locations for web-spinning spiders that prey on spruce budworm moths in Maine (see text for list of site abbreviations).

Most study sites were in cutover spruce-fir stands with abundant natural regeneration of balsam fir, *Abies balsamea* (L.) Mill., and red spruce, *Picea rubens* Sarg., or white spruce, *P. glauca* (Moench) Voss, in the understory. Observations were confined to accessible webs in small trees (most  $\leq 3$  m in height) and in lower crowns of intermediate-height trees ( $\leq 5.5$  m). All trees were in the understory and grew in forest openings, e.g., along old logging roads and trails. Forest-stand measurements were not taken; however, balsam fir was the prominent understory species.

**Study periods.**—We observed spider predation on spruce budworm moths during the peak years (1977-82) of a budworm epidemic in Maine. A few observations were made during the decline phase of the same epidemic in 1985. Each study year, webs of web-spinning spiders were examined for moth prey during the spruce budworm's moth-flight period. In Maine, budworm moth flight begins in late June, peaks in early to mid-July, and ceases by late July or early August (Houseweart et al. 1982; Kendall et al. 1982; Jennings et al. 1984). Male moths of the spruce budworm generally emerge from pupae 1 or 2 days earlier than female moths, and most moths live for about 10 days (Greenbank et al. 1980). Because of seasonal variation in development, moth activity at a site lasts about 3 weeks, but can be extended longer by invasion of dispersing moths (Greenbank et al. 1980). We made detailed observations every 2-10 days at three sites, Greenville (GRE), Medford (MED), and Penobscot Experimental Forest (PEF); observations at remaining sites were intermittent but within the budworm's moth-flight period.

**Predator-prey collections.**—At all study sites, we examined spider webs on understory coniferous trees *ad libitum* (i.e., as encountered) and collected both

spider(s) and any ensnared moth prey. Most of the spiders we studied in Maine either left cadavers of spruce budworm moths in their webs (*Frontinella*) or incorporated the cadavers into web retreats (*Theridion*). Occasionally, prey cadavers were found wrapped in silk and dropped below the web (*Theridion*), or hung in prey middens (*Cyclosa*), or hung in web supports (*Neoscona*). Some unwrapped prey were found discarded immediately below the web (*Prolinyphia*). To minimize disturbance, the resident spider was captured first and then prey removed from the web or substrate with forceps. Field-collected spiders and their prey were placed in 2-dram vials containing 70% ethanol, labeled, and transported to the laboratory for identification.

Not all available webs were examined at each site, nor were all observed spiders with budworm prey collected. However, when a spider-prey collection was made, we removed *all* spruce budworm moths from the web or immediately below the web. Our goal was to collect a representative sample of web-spinning spiders that captured spruce budworm moths in the readily accessible understory.

**Web surveys.**—In addition to predator-prey collections, we inventoried spider webs and their ensnared prey at various locations. Two survey methods were used to provide temporal and spatial replication.

1) *Temporal replication:* At Greenville (GRE), Medford (MED), and Penobscot Experimental Forest (PEF), webs of the two most commonly encountered species—*Frontinella pyramitela* (Walck.) and *Theridion pictum* (Walck.)—were identified and tagged on 20-22 small trees/site. Numbers of webs by species and site were: *F. pyramitela*—MED ( $n = 20$ ), PEF ( $n = 53$ ); *T. pictum*—GRE ( $n = 55$ ), MED ( $n = 10$ ). Both species spin their webs in young understory spruce or fir trees; each species builds a characteristic web. The sheetline weaver *F. pyramitela* spins a “bowl and doily” web consisting of a shallow bowl, a horizontal sheet beneath the bowl, and a meshwork of silk that forms a barrier above the bowl (Comstock 1948). The theridiid *T. pictum* constructs a tangle web of many viscid threads, above which the spider ties several spruce or fir needles together to form a dome-shaped tent in which to hide (Emerton 1927). Cadavers of spruce budworm moths and other prey often are incorporated into the silken walls of the tent; occasionally, prey is hung in the tangle web or dropped to branches below the web.

Tagged trees and webs were revisited at intervals of 2-10 days ( $\bar{X} = 5.5$  days) and data recorded on spider-web occupancy and prey captures. In most instances we gently removed all ensnared moths from the tagged webs for prey identification and prey-sex determination. There was minimal web disturbance. Occasionally however, budworm moths were field-identified (but not sexed), counted, and left intact in the webs. Tagged-web observations spanned the initial period (late June,  $n = 2$  visits/site) and peak (mid-July,  $n = 3-4$  visits/site) in spruce budworm moth-flight activity.

2) *Spatial replication:* At each of the aforementioned sites plus Howland (HOW), Coffeelos (COF), and Telos (TEL), 30 webs (any species) were examined *ad libitum* and numbers of budworm prey/web recorded. Field identifications were made of *F. pyramitela* and *T. pictum*; specimens of unrecognized species were collected for later identification. Cadavers of spruce budworm moths were removed from webs for prey-sex determination. All 30-web inventories (1-3/site) were made during the spruce budworm's moth-flight period in late June ( $n = 2$ ) and July ( $n = 7$ ).

**Tree-web heights.**—At some study sites, measurements were taken of tree and web height (m) above ground for *F. pyramitela* and *T. pictum*. Tree height was measured from ground to uppermost terminal-shoot level; web height was measured from ground to bowl level (*Frontinella*) and tent level (*Theridion*).

**Spider identifications.**—Collected spiders were identified by the senior author; species determinations follow Kaston (1981) and other consulted sources including revisions by Chamberlin and Gertsch (1958), Berman and Levi (1971), and Levi (1957, 1974). Only sexually mature spiders were identified to species; juveniles, including penultimate males, were identified to generic level. Representative specimens of all identified species are deposited in the arachnid collection, U.S. National Museum of Natural History, Washington, DC.

**Prey-sex determinations.**—All moth cadavers removed from spider webs were examined microscopically and their genitalia compared with published descriptions of the male (Outram 1970) and female (Outram 1971) reproductive systems of the spruce budworm. Such examinations allowed confirmation of field-identified prey species and determination of prey sex. A few collected moths (< 5%) were devoid of genitalia, i.e., the posterior abdominal segments were missing—possibly lost during collection, discarded by the spider, or removed by scavengers. Remains of these damaged moths were identified by their general morphology (Freeman 1947) and compared with known, identified specimens; they were sexed by tibial-spur length (long, male; short, female) and shape of the scutellum.

**Data analyses.**—Because the spruce budworm has a sex ratio that does not vary markedly from 1:1 (Miller 1963), we hypothesized an equal representation of the sexes (male, female) among budworm moth-prey captured by web-spinning spiders. We used the *G*-statistic for log-likelihood ratios (Sokal and Rohlf 1981) to test observed vs. expected frequencies of moth sexes among prey captures for individual and over all spider species. The null hypothesis for expected frequency was 50% male, 50% female moths. Resultant *G*-values were compared with the chi-square distribution at  $P = 0.05$ .

Means, standard errors, and coefficients of variation were calculated for tree- and web-height measurements for *F. pyramitela* and *T. pictum*. We also calculated relative web height (Toft 1987) for both species by the formula: rel. web ht. = web ht./tree ht.  $\times$  100. The Wilcoxon's two-sample test (Sokal and Rohlf 1981) was used for comparisons of means (tree ht., web ht., rel. web ht.) between spider species at  $P = 0.05$ . Spearman's rank correlation coefficient ( $\rho$ ) was used to determine the degree of association between tree- and web-height variates for each species.

## RESULTS

**Spider taxa.**—Web-spinning spiders of 6 families, 12 genera, and at least 15 species were observed with spruce budworm moth prey in Maine (Table 1). Almost all of the budworm prey captures were made by female spiders; a single male of *Agelenopsis utahana* (Chamberlin & Ivie) was collected with budworm-moth prey; a few webs of *F. pyramitela* (1), *Prolinyphia marginata* (C. L. Koch) (2) and *Theridion murarium* Emerton (1) were cohabited by both spider sexes and contained cadavers of spruce budworm moths. At Medford (MED), we

Table 1.—Species of web-spinning spiders observed for spruce budworm moth prey, 18 localities, spruce-fir forests of Maine; all study years combined. The *G*-statistic for log-likelihood ratios (Sokal and Rohlf 1981) was used to compare observed vs. expected frequencies of moth sexes among prey captures (loc = localities, obs = observed, SBW = spruce budworm, ns = not significant,  $P > 0.05$ , \* = includes multiple observations of some webs).

FAMILY Species	n webs		n webs with SBW prey	Σ SWB prey		<i>G</i>	<i>P</i>
	n loc	obs		Males	Females		
AGELENIDAE							
<i>Agelenopsis utahana</i> (Chamb. & Ivie)	1	1	1	1	0	1.39	ns
<i>Agelenopsis</i> sp.	2	2	2	3	0	4.16	≤0.05
ARANEIDAE							
<i>Araneus nordmanni</i> (Thorell)	1	1	0				
<i>Araneus marmoreus</i> Clerck	1	1	0				
<i>Araneus</i> sp.	4	5	3	3	0	4.16	≤0.05
<i>Araniella displicata</i> (Hentz)	5	6	4	4	0	5.54	≤0.05
<i>Cyclosa conica</i> (Pallas)	5	10	3	3	0	4.16	≤0.05
<i>Cyclosa</i> sp.	1	3	0				
<i>Neoscona arabesca</i> (Walck.)	3	10	1	0	1	1.39	ns
<i>Neoscona</i> sp.	7	31	28	35	2	35.73	≤0.001
<i>Nuctenea patagiata</i> (Clerck)	1	1	1	1	0	1.39	ns
<i>Nuctenea</i> sp.	1	1	1	1	0	1.39	ns
DICTYNIDAE							
<i>Dictyna phylax</i> Gertsch & Ivie	1	1	1	1	0	1.39	ns
<i>Dictyna</i> sp.	1	1	1	1	0	1.39	ns
LINYPHIIDAE							
<i>Frontinella pyramitela</i> (Walck.)	14	420*	98	129	9	124.77	≤0.001
<i>Pityohyphantes costatus</i> (Hentz)	7	11	8	9	0	12.48	≤0.001
<i>Pityohyphantes</i> sp.	5	7	0				
<i>Prolinyphia marginata</i> (C.L. Koch).	7	31	18	18	2	14.72	≤0.001
<i>Prolinyphia</i> sp.	1	1	0				
TETRAGNATHIIDAE							
<i>Tetragnatha versicolor</i> Walck.	4	6	2	2	0	2.77	ns
THERIDIIDAE							
<i>Theridion differens</i> Emerton	4	26	4	5	1	2.91	ns
<i>Theridion frondeum</i> Hentz	4	5	3	3	1	1.05	ns
<i>Theridion murarium</i> Emerton	12	17	10	8	5	0.70	ns
<i>Theridion pictum</i> (Walck.)	11	564*	172	175	28	118.53	≤0.001
<i>Theridion</i> spp.	2	8	0				
All species	18	1170*	361	402	49	315.22	≤0.001

observed a male and female of *P. marginata* sharing prey, i.e., both spiders were feeding on the same male budworm moth. Juveniles of *Agelenopsis*, *Araneus*, *Dictyna*, *Neoscona*, and *Nuctenea* were observed with budworm moth prey, whereas juveniles of *Cyclosa*, *Pityohyphantes*, *Prolinyphia*, and *Theridion* were not.

**Moth-prey numbers.**—Numbers of budworm moths/web ranged from 1-5 for *F. pyramitela*, and from 1-14 for *T. pictum*; numbers for the remaining species

seldom exceeded 2 moths/web. For multiple observations of the same web (temporal replication), mean budworm moths/web was significantly higher ( $Z = -4.36$ ,  $P = 0.000$ ) for *T. pictum* ( $\bar{X} = 0.41 \pm 0.07$ ,  $n = 301$ ) than for *F. pyramitela* ( $\bar{X} = 0.07 \pm 0.02$ ,  $n = 168$ ). However, such differences in prey-capture rates between spider species were not detected ( $Z = -1.49$ ,  $P = 0.14$ ) when several localities (spatial replication) were considered; *F. pyramitela* ( $\bar{X} = 0.52 \pm 0.05$ ,  $n = 252$ ) and *T. pictum* ( $\bar{X} = 0.63 \pm 0.06$ ,  $n = 263$ ).

**Moth-prey sex.**—A total of 402 male and 49 female moths of the spruce budworm were collected from spider webs (all species) in Maine (Table 1). Most of the budworm moths were retrieved from webs of *F. pyramitela* (30.6%) and *T. pictum* (45.0%). Male spruce budworm moths were captured by at least 15 species of web-spinning spiders, whereas female budworm moths were captured by only 7 species of web spinners. At least 9 (18.4%) of the ensnared female moths were freshly emerged and gravid; most were captured by species of *Theridion*, i.e., *T. pictum* ( $n = 5$ ), *T. murarium* Emerton ( $n = 2$ ), and *T. frondeum* Hentz ( $n = 1$ ). The *T. frondeum* capture was a male-female pair *in copula*; the gravid female moth was dead whereas the male was still alive when observed and collected.

*G*-tests indicated that significantly more ( $P \leq 0.05$ ) male than female moths of the spruce budworm were captured by at least nine species of web-spinning spiders (Table 1). The overall species total was significantly biased ( $P \leq 0.001$ ) toward capture of male spruce budworm moths. This differential mortality to male moths of the spruce budworm previously has not been discovered and reported.

**Web surveys.**—Because there were no significant differences in percentages of webs with budworm prey by survey method, we pooled the data from web-inventory sources. Over all spider species ( $n = 11$  observed during surveys), study-site locations ( $n = 6$ ), and observation dates ( $n = 15$ ), the mean percentage of webs with spruce budworm moths was  $15.99 \pm 2.69$ . Mean percentages of *F. pyramitela* and *T. pictum* webs with budworm prey were  $19.49 \pm 5.73$  and  $18.89 \pm 3.56$ , respectively. The arcsine transformed means for these two species were not significantly different (Wilcoxon 2-sample test,  $Z = 1.38$ ,  $P = 0.17$ ). Because percentages of webs with budworm prey ranged from 0-100 for some dates, the coefficients of variation were high over all species (166.77) and for both *F. pyramitela* (158.42) and *T. pictum* (92.47). Such variation was also evident when web percentages were plotted by observation date (Fig. 2) for these two species. Percentages of *T. pictum* webs with budworm moths peaked in early July and remained at a relatively high level ( $\cong 20\%$ ); *F. pyramitela* webs declined sharply after an initial peak in mid-July.

**Tree-web heights.**—Tree height for *F. pyramitela* ranged from 0.6-5.5 m; web heights for this species ranged from 0.3-2.1 m. Correspondingly, tree heights for *T. pictum* ranged from 1.0-4.6 m; web heights ranged from 0.3-2.3 m. Tree- and web-height means were significantly different ( $Z = 7.62$ , tree;  $Z = 4.31$ , web) between species (Table 2); trees occupied by *T. pictum* were significantly taller ( $P = 0.000$ ) and webs significantly higher ( $P = 0.000$ ) than those of *F. pyramitela*. Mean relative web height was  $> 60\%$  of tree height for both species; however, mean percentages were not significantly different ( $Z = -1.05$ ,  $P = 0.29$ ) between species (Table 2). Spearman's rank correlation coefficients indicated a greater degree of association between web and tree heights for *F. pyramitela* ( $\rho = 0.58$ ,  $P \leq 0.001$ ) than for *T. pictum* ( $\rho = 0.24$ ,  $P \leq 0.006$ ). However, relative web height

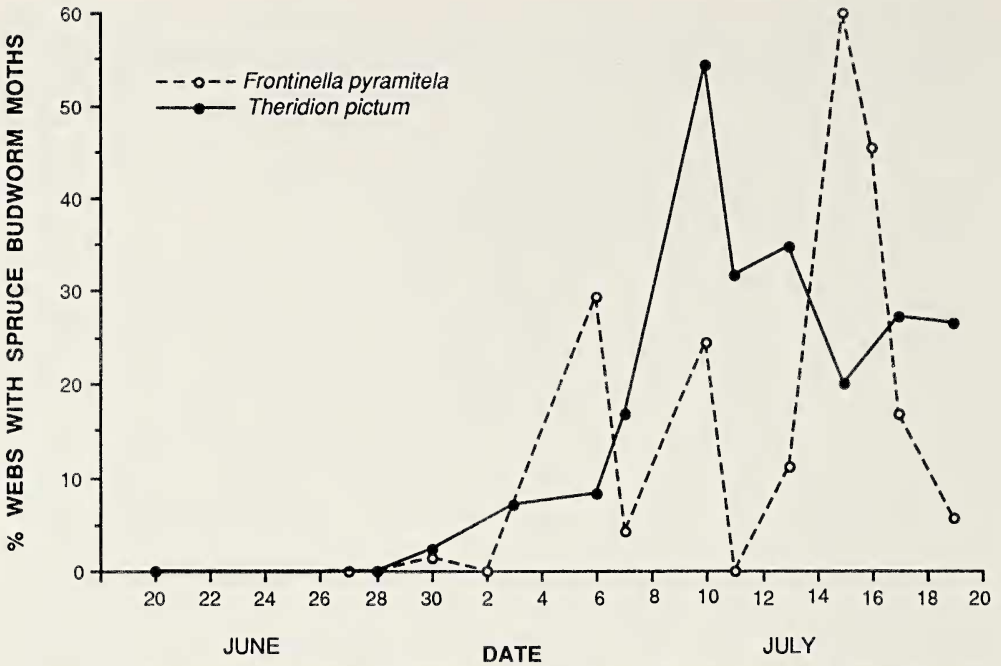


Figure 2.—Percentages of *Frontinella pyramitela* and *Theridion pictum* webs with spruce budworm moth prey by observation date; study sites and years combined.

was negatively correlated with tree height for *T. pictum* ( $\rho = -0.53$ ,  $P \leq 0.001$ ) and less so for *F. pyramitela* ( $\rho = -0.13$ ,  $P \leq 0.13$ ).

Next we considered tree, web, and relative web-height means for both species by prey-capture category (with, without budworm moth prey). For *F. pyramitela*, none of the means were significantly different between prey-capture category (Table 3); tree heights ( $Z = -1.82$ ,  $P = 0.07$ ), web heights ( $Z = -1.24$ ,  $P = 0.22$ ), relative web height ( $Z = -0.74$ ,  $P = 0.46$ ). For *T. pictum*, mean tree height was significantly taller ( $Z = -2.58$ ,  $P = 0.009$ ) for webs with budworm moths; however, web-height means did not differ significantly ( $Z = 0.31$ ,  $P = 0.76$ ) between prey-capture category. Mean relative web height was significantly less ( $Z = 2.46$ ,  $P = 0.01$ ) for *T. pictum* webs that captured spruce budworm moths (Table 3), possibly because tree height was significantly taller for these successful webs.

**Kleptoparasites.**—At least two species of kleptoparasites (Theridiidae) were observed and collected; *Argyrodes trigonum* (Hentz) from webs of *F. pyramitela* ( $n = 4$ ), *T. pictum* ( $n = 2$ ), and *Neoscona* sp. ( $n = 1$ ); *Argyrodes fictilium* (Hentz) and *Argyrodes* sp. each from webs of *F. pyramitela* ( $n = 2$ ). Specimens of *A.*

Table 2.—Comparisons of mean ( $\pm$  SE) tree, web, and relative web heights of *Frontinella pyramitela* and *Theridion pictum*, northeastern spruce-fir forests, Maine. Relative web height = web ht./tree ht.  $\times$  100. Column means followed by different letters (a, b) are significantly different by Wilcoxon 2-sample test,  $P = 0.05$  (SAS Institute 1985).

Spider species	n	Tree ht. (m)		Web ht. (m)		Rel. web ht. (m)	
		$\bar{X}$	( $\pm$ SE)	$\bar{X}$	( $\pm$ SE)	$\bar{X}$	( $\pm$ SE)
<i>Frontinella pyramitela</i>	146	1.67a	0.05	1.06a	0.04	65.11a	1.76
<i>Theridion pictum</i>	134	2.14b	0.04	1.29b	0.03	62.61a	1.63



Table 3.—Comparisons of mean ( $\pm$  SE) tree, web, and relative web heights of *Frontinella pyramitela* and *Theridion pictum* by web-prey category, northeastern spruce-fir forests, Maine. Relative web height = web ht./tree ht.  $\times$  100. Column means (within species) followed by different letters (a, b) are significantly different by Wilcoxon 2-sample test,  $P = 0.05$  (SAS Institute 1985).

Spider species	n	Tree ht. (m)		Web ht. (m)		Rel. web ht. (m)	
		$\bar{X}$	( $\pm$ SE)	$\bar{X}$	( $\pm$ SE)	$\bar{X}$	( $\pm$ SE)
<i>Frontinella pyramitela</i>							
with budworm moths	26	1.58a	0.19	0.98a	0.10	63.36a	3.31
without budworm moths	120	1.69a	0.05	1.08a	0.04	65.49a	2.02
<i>Theridion pictum</i>							
with budworm moths	83	2.22a	0.05	1.28a	0.04	59.18a	1.82
without budworm moths	51	2.02b	0.08	1.30a	0.05	68.18b	2.95

*trigonum* were collected at PEF, MED, T18, T19, and P14; *A. fictilium* and *Argyrodes* sp. were found only at MED. Most (72.7%,  $n = 11$ ) of these kleptoparasites were associated with host-spider webs that had successfully captured male moths of the spruce budworm (1-3 moths/web). We did not observe *Argyrodes* spiders feeding directly on budworm prey.

## DISCUSSION

**Spider habitat associations.**—The species of web-spinning spiders that we collected from understory balsam fir and spruce differ markedly from the terricolous spider fauna of Maine's spruce-fir forests (Jennings et al. 1988; Hilburn and Jennings 1988). However, many of the understory species also are known to inhabit crowns of mature trees. For example, *Araniella displicata* (Hentz), *Pityohyphantes costatus* (Hentz), *Dictyna phylax* Gertsch & Ivie, and *Theridion murarium* Emerton have been collected from crowns of dominant/codominant red spruce and balsam fir in Maine (Jennings and Collins 1987; Jennings and Dimond 1988). The orb weaver *Cyclosa conica* (Pallas) was found in foliage samples clipped from crowns of mature red spruce in Maine (Jennings and Dimond 1988); webs of this species also are found suspended between small trees in the understory. Species common to arboreal habitats of mature tree crowns and to small, understory tree strata of Maine's spruce-fir forests include *Araniella displicata*, *Dictyna phylax*, *Tetragnatha versicolor* Walckenaer, and *Theridion differens* Emerton.

Interestingly, the two species that we most commonly observed with budworm moth prey, *F. pyramitela* and *T. pictum*, apparently prefer the herb-shrub-small tree-zone in spruce-fir forests of Maine. Neither species has been taken in pitfall traps (Jennings et al. 1988; Hilburn and Jennings 1988), or among extensive foliage samples clipped from crowns of dominant/codominant red spruce (Jennings and Collins 1987), balsam fir, red and white spruce (Jennings and Dimond 1988), and hemlock (Jennings, unpublished data). In Maine's spruce-fir forests, webs of *F. pyramitela* most frequently are found on small trees and shrubs, and occasionally on low-growing forbs ( $\leq 0.3$  m). Webs of *T. pictum* most commonly are found on small trees, less frequently on shrubs, and seldom on low-growing forbs in these forests.

Our data on web heights and relative web heights for *F. pyramitela* and *T. pictum* (Table 2) indicate a possible nonrandom selection of foraging patch by

both species, i.e., mean relative web height was  $> 60\%$  of tree height for both species. And both species built their webs near branch apices where flying insects are apt to alight; webs of neither species were seldom observed within interiors of tree crowns. Selection of foraging patches near branch tips may favor predation on male moths of the spruce budworm because males "buzz" (i.e., slow, hovering flight) near the periphery of branches and near tree crowns (Sanders and Lucuik 1972; Greenbank et al. 1980). Other species of web-building spiders are known to make web-site selections based on prey abundance; see Riechert and Gillespie (1986) for a review on nonrandom selection of foraging patch by spiders.

**Sex-biased predation.**—Our observations over several years indicate that male moths of the spruce budworm are much more susceptible to predation by web-spinning spiders than female moths of this coniferous-tree defoliator, at least in the understory. We have no data on possible budworm-moth predation by web-spinning spiders that inhabit mature tree crowns; however, such predation is likely to be extensive, especially during budworm epidemics, because of the high densities of both spiders (Jennings and Collins 1987) and budworms (Morris 1955) found in crowns of mature conifers. For small coniferous trees in the understory, the current study confirms that significantly more ( $P \leq 0.05$ ) male than female moths of the spruce budworm are captured by at least nine species of web-spinning spiders. The factors that cause and influence this differential mortality to male moths of the spruce budworm are unknown. We consider and discuss the following possibilities: 1) attraction of male moths of the spruce budworm to prey-mimicking pheromones emitted by spiders; 2) uneven densities and distributions of male-female moths in the understory; 3) accidental capture of male moths responding to "calling" female moths located near spider webs; 4) differences in male-female moth behavior; and 5) sexual differences in flight activities of spruce budworm moths. These factors are not necessarily independent, but may be interactive.

1) *Sex-pheromone mimicry*: There is mounting evidence that some spiders produce compounds that attract male moths (Hacker 1935; Eberhard 1977; Horton 1979; Yeargan 1988); the elicited responses are similar to the effects caused by sex pheromones of target prey species (review in Stowe 1986). Most observations of sex-pheromone mimicry concern species of araneid spiders that attract and capture only male moths; attracted Lepidoptera include species of Geometridae, Noctuidae, Pyralidae, and Olethreutidae (Stowe 1986), and Saturniidae (Horton 1979). Apparently, the ability to mimic sex pheromones of moths has evolved more than once (Stowe 1986), and the attractants emanate from the spiders (Eberhard 1977; Stowe 1986; Stowe et al. 1987) or from their webs (Horton 1979; Eberhard 1981). The preponderance of male budworm moths captured in spider webs in Maine suggests that sex-pheromone mimicry might be involved; however, field bioassays of male-moth attraction and olfactory-choice studies are needed to confirm such mimicry. Conversely, the capture of both male and female moths in some webs, and the apparent lack of prey specialization (i.e., captures included Homoptera, Diptera, Coleoptera, and Lepidoptera), lends minimal support to a sex-pheromone mimicry hypothesis. Additionally, several species of spiders of diverse families (Table 1) captured male moths of the spruce budworm; thus far, sex-pheromone mimicry by spiders has been confirmed for only a select few species, mostly Araneidae (Stowe 1986).

2) *Uneven prey densities*: Virtually nothing is known about the density and distribution of spruce budworm moths in the understory of spruce-fir forests. During outbreaks, small understory trees are defoliated by budworm larvae, and female moths deposit some eggs on needles of understory trees (Morris 1955; Jennings and Jones 1986). Most observations of spruce budworm moths concern dispersal flights and estimates of aerial densities of moths above the forest canopy (Greenbank et al. 1980). Measurements of moth densities within forest stands are extremely difficult because of intervening foliage layers, moth-flight activities, and differential responses of moth sexes to light traps (Greenbank et al. 1980). Despite these limitations, investigators have noted a markedly consistent 50% male: 50% female ratio for the budworm population in stands over the season (Miller 1963; Greenbank et al. 1980). However, exodus flights (emigration) from forest stands and mass invasions (immigration) of budworm moths into stands contain a high proportion of egg-carrying female moths (Greenbank et al. 1980). Because invading moths often drop to the ground, such invasions may affect moth densities in the understory. But in Maine, we never witnessed a mass invasion of moths at any study site. Although we cannot exclude possible unequal distributions and densities of moth sexes in the understory, we suspect that sexual differences in behavior and moth-flight activities were more influential in affecting sex-biased predation by web-spinning spiders.

3) *Accidental capture*: Sex-pheromone communication by the spruce budworm has received a great deal of attention from investigators (Sanders 1971, 1975; Sanders and Lucuik 1972, 1975), but the possible interrelationships between "calling" female moths and predators has not been studied. We suspect that the increased activities of male moths responding to sex pheromones greatly magnifies their chances of capture by web-spinning spiders. Spider webs *in situ* near "calling" female moths are apt to capture the most male moths; however, this hypothesis needs to be tested under field conditions. Female moths of the spruce budworm emerge from pupae in midafternoon (Sanders and Lucuik 1972), and remain sedentary near their place of emergence (Sanders 1975). The female moths start "calling" near dusk and continue calling throughout the night (Sanders 1971, 1975). Hence, female moths that emerge and emit sex pheromones near spider webs are apt to attract potential prey to these webs. The "buzzing" flight activity of male moths is continuous throughout the day but increases in intensity by mid-afternoon (Sanders and Lucuik 1972), and corresponds with the peak calling activity of female moths (Sanders 1971). Although we did not measure hourly capture rates for spider webs in Maine, we suspect that most moths were caught during the time of increased male-moth activity. We often observed spruce budworm moths flying into spider webs and being captured successfully by resident spiders during daylight hours; no observations were made at night.

Newly emerged, mated female moths of the spruce budworm also remain sedentary near their place of emergence (Sanders and Lucuik 1975) and call intermittently on successive days (Sanders and Lucuik 1972). Hence, spider webs *in situ* near such resident female moths may make multiple moth captures on successive days. This might explain why some webs captured male moths successfully during more than one observation period in Maine.

4) *Moth behavior*: Recent studies have shown that some insects are attracted to ultraviolet (UV) light reflected from spider webs (Craig and Bernard 1987);

however, such attraction has not been demonstrated for spider webs and spruce budworm moths in northeastern spruce-fir forests. The "buzzing" flights of male moths, from dawn until shortly after midnight (Greenbank et al. 1980) and near tree-crown peripheries within centimeters of branch tips (Greenbank 1973), suggests that: (a) male moths are active during the diurnal period of greatest light reflectance, and (b) male moths frequent zones where spider webs are common (i.e., near branch apices). Further, flying male moths of the spruce budworm are consistently photopositive to a discrete light source, whereas female moths generally are photonegative (Wellington 1948). These behavioral differences, coupled with heightened male moth-flight activity, might explain why male moths are more susceptible to predation by web-spinning spiders. Phototactic responses of male and female moths to UV-reflected light emanating from spider webs need to be tested in northeastern spruce-fir forests.

5) *Moth-flight activity*: Finally, greater male than female moth-flight activity probably is the factor that contributes most to spider predation on spruce budworm moths. Increased levels of potential prey activity should greatly influence the foraging success of "sit and wait" predators like some web-spinning spiders. Male moths of the spruce budworm are more active, both spatially and temporally, than female moths (Greenbank et al. 1980); such activity increases the likelihood of male-moth encounters with spider webs, and particularly with webs built near branch apices where male moth-flight activity is high. In laboratory experiments with spiders preying on aphids, Provencher and Coderre (1987) concluded that the most active prey, not necessarily the most abundant, will be the most captured. Because female moths of the spruce budworm generally remain sedentary, with few short, interbranch flights until 50% of their eggs are laid (Greenbank et al. 1980), female-moth encounters with spider webs initially are reduced. Males and spent females of the spruce budworm are more active than gravid females (Greenbank et al. 1980).

We conclude that the minimal flight activities of female moths after emergence reduces their susceptibility to spider predation—at least by web-spinning species. Conversely, the intensified flight activities of male moths—whether induced by sex-mimicking pheromones, moth sex pheromones, or UV-reflected light—increases their susceptibility to spider predation. Quantification of potential prey activities and their influences on spider predation need further investigation.

**Web surveys.**—The peaks in percentages of *F. pyramitela* and *T. pictum* webs with budworm prey (Fig. 2) generally coincide with peaks in pheromone-trap catches of spruce budworm moths in Maine's spruce-fir forests (Houseweart et al. 1981; Jennings et al. 1984). These results support our hypothesis that male-moth activity plays a significant role in predation by web-spinning spiders. Because pheromone traps measure male moth activity (Sanders 1971), daily trap catches may be useful for predicting captures of spruce budworm moths by web-spinning spiders. This assumes that predation by web-spinning spiders on spruce budworm moths is both density and activity dependent.

Future web surveys should take into account differences in web-residence times of host spiders; unoccupied webs are less likely to capture spruce budworm moths than occupied webs. During our sequential visits to tagged webs in Maine, we noted that as time progressed, *F. pyramitela* webs were more likely to be unoccupied than *T. pictum* webs. In New Jersey, Janetos (1984) observed a mean residence time of only 5.4 days for *F. pyramitela*. Scavenging of moth prey from

spider webs by ants and kleptoparasites also may confound survey results, i.e., underestimate predation by web-spinning spiders. Because some theridiid spiders feed on ants, ants may be more successful at removing budworm moths from sheetwebs of *F. pyramitela* than from tangle webs of *T. pictum*. Ants were included among the prey items removed from *T. pictum* webs in Maine.

**Kleptoparasitism.**—In addition to stealing prey from host spiders, Trail (1980) observed araneophagy by species of *Argyrodes*; the kleptoparasite attacks and kills the host spider (Wise 1982). Because of systematic destruction of several host spiders, Shear (1986) concluded that *A. fictilium* may be a specialist on *Frontinella communis* (Hentz) (= *F. pyramitela*). However, in Maine we found *A. trigonum* more commonly associated with *F. pyramitela* webs; only one specimen of *A. fictilium* was collected. Rypstra (1981) indicated that *Argyrodes* spiders may cause the host spider to move its web. We suspect that some of the web “abandonments” in Maine may be attributed to invasion and occupancy by *Argyrodes*, and possibly host-spider mortality induced by these kleptoparasites. For example, *Argyrodes* spiders were observed in 3 of 4 webs “abandoned” by *T. pictum* at MED. Both species of *Argyrodes* found during this study, *A. trigonum* and *A. fictilium*, have been recorded from Maine (Exline and Levi 1962).

**Spider-budworm impacts.**—What are the overall effects of spider predation on spruce budworm moths? Does sex-biased predation on male moths adversely affect the reproductive potential of the spruce budworm, and, consequently, population trend for the next generation? These and other questions need to be answered. This study shows that web-spinning spiders cause differential mortality to male moths of the spruce budworm; however, the consequences of such mortality on population dynamics of the budworm are unknown.

Predation by web-spinning spiders on male moths could hamper mating success and reproductive potential of the spruce budworm. Male moths of the spruce budworm mate only once, and female moths rarely mate more than once *per 24-h period* (Sanders 1975). Although males are capable of multiple matings (i.e., with more than one female), an increasing proportion of second and subsequent matings are infertile (Outram 1971). It follows then that significant mortality to male moths increases the likelihood that virgin female moths will remain unmated or be inseminated by “experienced” males with reduced fertility. Both unmated females and females from infertile matings of the spruce budworm lay few eggs (Outram 1971); hence, female oviposition success and reproductive potential are indirectly affected by male-moth survivorship. Likewise, predation on gravid female moths and moths *in copula*, as observed in this study, directly influences reproductive potential of the spruce budworm. Because of these potential impacts on spruce budworm reproduction, predation by spiders gains increased importance as a source of moth mortality. Additional studies are needed to assess age-interval survivorships of both predators and prey.

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